

THE UNIT OF GENETIC CHANGE IN ADAPTATION AND SPECIATION

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ABSTRACT

Genetic variability in natural populations is very great. To a large degree, the types of variation found reflect the methods used. Thus we may recognize, segregating in natural populations, (1) point mutations (oligogenes) which have visible or physiological effects, (2) lethal and semilethal genes, (3) chromosome aberrations, and (4) soluble protein variability. This paper adduces cases which suggest that evolutionary change (adaptation or speciation or both) can occur without significant participation by any of the four classes of variation listed above. Thus, some cases of newly-formed species are known in which the species pair is chromosomally homosequential. Other cases show very little soluble protein (allozyme) difference (similarity coefficients of 0.95 or higher). These species appear to be much more newly formed than the classical "sibling" species of the *obscura* or *willistoni* groups of *Drosophila*. Nor does their biochemical similarity mean that such species differ by only a few genes. Rather, the genetic differences which characterize species when they are first formed may be numerous and largely of a regulatory nature. New recombinationally-synthesized blocks of epistatically interacting polygenes may also characterize newly-formed species. A theory that the amount of soluble protein change is primarily a function of time since the separation of two lineages is presented. This is apparently supported by allozyme data on eight species of *Drosophila* inhabiting Hawaiian islands of successively younger times of origin.

Ten years ago, systematic and evolutionary biology suddenly found itself wedded to molecular genetics. This strange affair came about because of the application of the new electrophoretic techniques to the genetic state of individuals in natural and artificial populations. The effect of this new biochemical genetics has been galvanic, especially in population genetics. Although traditionally strong in theory, this field had been struggling along for years with techniques of genetic analysis which could be applied to only a few kinds of organisms. Under the influence of these new techniques, however, both systematics and ecology have become deeply involved in a biochemical approach. Revolutionary ideas have been popping up on every hand. The purpose of the present discussion is to take a brief look back over the last few eventful years to see if major new concepts may be discerned.

ADAPTATION

How does the natural genetic variability within a species relate to the immediate needs of the organism? To what extent do the genes track the environment? First to be discovered were the recessive "visible" mutations which can be segregated out, from specimens collected in the wild, by inbreeding their progeny in the laboratory. Following this, variants which are manifested cytologically, like inversions and translocations, came to light. Many of these were shown to exist as balanced polymorphisms in nature. Still later, as genetic techniques became more sophisticated, precise methods revealed a further wealth

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of variability based on recessive lethal genes, which were also shown to be carried widely in natural populations. Then came renewed emphasis on polygenic variability, a source of variation which had been long exploited by the animal and plant breeder. There is no question that a large store of polygenic genetic variability also characterizes natural populations. Laboratory, population-cage and field-plot selection experiments have revealed the reality and ubiquity of these polygenic systems (for a recent review, see Mather, 1973).

Then Markert's ingenious and simple starch-gel techniques came to be applied to natural populations. This trend developed into a virtual orgy of biochemical research as allozyme and other soluble protein variation has been catalogued in populations of mice, horseshoe crabs, elephant seals, wild oats and, of course, many, many kinds of *Drosophila*. The majority of the loci that encode for soluble proteins show levels of polymorphism and individual heterozygosities which are almost universally high. The amount of data generated in the last few years boggles the mind.

Perhaps because biochemical data are glamorous or because the methods are so elegantly simple, soluble protein variability seems now to be considered consonant with, or at least representative of, genetic variability in the broad sense. Thus, in the current literature, "genetic variation" and "genetic similarity" are used as synonyms of "electrophoretic variability" (or similarity). By inference, the other types of genetic variability seem to have been assigned relatively minor roles and biochemical variation assigned a major one. In the flush of excitement over allozymes, it sometimes seems that the other types of genetic variability have been partially forgotten. The time seems right for a revival of interest in these other types of genetic variability.

The present article attempts a review of the relative importance of these various sorts of genetic variability with regard to the dynamic changes in populations that we call the evolutionary process. My general theme is that neither the soluble proteins nor the structural chromosome changes satisfy the requirements for the genetic variability which is related to adaptation. The most important variation seems to be that generated by recombination from the polygenic systems and the regulatory genes which control them.

The adaptive process takes place only at one point in nature; that is, within the local population, or deme. Furthermore, it can occur only in a population which maintains a genetically variable gene pool. Under natural selection, the genetic composition of the population shifts in response to environmental demands. As an intrademic process, occurring in time, such tracking of the environment is basically phylogenetic in the sense that the population passes as a whole from one genetic composition to another during passage of time. This type of change is sometimes referred to as anagenesis, as contrasted with cladogenesis, a process in which the population splits and then becomes genetically different in its different branches.

A number of natural and experimental instances of environmental tracking are well known. I refer to such cases as industrial melanism in moths, copper tolerance in plants, DDT resistance in insects, and antibiotic resistance in microorganisms. A recent striking case of copper resistance in *Paramecium* has been

described by Nyberg (1975). One may also cite the many accomplishments of the plant and animal breeders whose engineering is simply applied microevolution.

Whereas the reality of these changes at the genotypic level cannot be doubted, considerable question remains as to exactly what kind of genetic alteration occurs as the population responds. In a number of instances, of course, the frequencies of specifically recognizable genes are changed; certain alleles may, in fact, become fixed. This result has been taken as a basic model of evolutionary change. In 1957, Haldane wrote: "The principal unit process in evolution is the substitution of one gene for another at the same locus."

On the other hand, significant genetic change under selection can occur with only minor change in gene, inversion, lethal, or allozyme frequency. The result cannot always be described as simply as Haldane's dictum suggests. Rather, selection appears to be favoring a new balanced combination of genes, an interacting and flexible unit. Kenneth Mather, a leading proponent of this theory for 30 years, long ago (1943) invoked the idea of both internal and relational balance. Through recombination at meiosis and syngamy, the genetic architecture of an organism usually rests at an equilibrium determined by opposing selective forces. When a new directional selective force is applied, effects are manifold throughout the genotypic system. Genetic recombination is viewed as a force which generates new gene combinations, always tending to perturb the status quo. A novel selective force may favor some of the products of this perturbation, causing the balance to shift to a new equilibrium. Simple substitution at a locus is seen only rarely.

The theory of coadaptation of genes, advanced by Dobzhansky, Wallace, and others as an explanation for balanced polymorphisms, bears considerable similarity to the balance theories of Mather. Thus shifting polymorphisms involving inversions, visibles, or allozymic loci in natural or experimental populations may all be viewed as changes which reflect shifts in gene interaction. Attention in these theories moves away from the single locus reacting in isolation. On the other hand, it emphasizes the shift in balance within the system. Even if not explicitly stated, shifting balance theory underlies much of the data of evolutionary genetics.

Considerations of this sort, furthermore, render the now waning "neutralist vs. selectionist" controversy somewhat meaningless. The views of both protagonists appear to oversimplify by treating the single gene as the unit of anagenetic evolutionary change.

On the other hand, Franklin & Lewontin (1970) and Lewontin (1974) have discussed what they call the "unit of selection." They suggest that in many, if not most, cases selection cannot be so simple as to favor a single-locus zygotic state, as if it were isolated in a neutral background. If there is value in such a view, it means that selection may indeed force a gene frequency change at an electrophoretically-detected locus, for example, without directly favoring or disfavoring the immediate gene product of that locus (e.g., see Stam, 1975). Changes in gene frequency may thus be correlated because it is the interacting system as a whole which is the unit of selection. Linkage is a powerful genetic force and may

be invoked, as Mather has done, to explain the many synergistic effects elsewhere in the organism when selection is artificially placed on a single character such as sterno-pleural bristle number in *Drosophila* (see the classic paper of Mather & Harrison, 1949).

Linkage disequilibrium, which is a manifestation of strong organizational forces operating on the balances and interactions of genes, has, in fact, been rather widely reported. Numerous cases are known, for example, where two or more linked inversions are held out of equilibrium by what are apparently strong selective forces (see Levitan, 1958, for review); striking cases are reported by Stalker (1960, 1964) and Sperlich & Feuerbach-Mravlag (1974). Perhaps it should be stressed that these cases are of disequilibrium *between* inversions. The inversion itself, of course, has well-known properties which lead to association of genes within it into a supergene (see Dobzhansky, 1959). This is indeed association, but it is not quite the same as the case when two or more inversions in the same chromosome show linkage disequilibrium. It is possible that the latter reflects a major organization of the genetic system rather than a property peculiar to simple recombination-blockage by an inversion.

Disequilibria in the absence of inversions are particularly crucial, in that they reveal associations which are maintained in the absence of any of the widely-recognized bars to crossing-over. Very clear cases have been adduced by Cannon (1963), Zouros & Krimbas (1973), Sinnock & Sing (1972), Charlesworth & Charlesworth (1973), and Roberts & Baker (1973). Mukai et al. (1974) have shown disequilibria between certain isozyme loci and adjacent inversions. Jones & Yamazaki (1974) have shown that linkage disequilibrium can affect allozyme frequencies in an experimental situation. In view of the technical difficulties attendant on the recognition of such systems these cases seem quite numerous. The theoretical work on the dynamic aspects of such systems (e.g., Lewontin & Kojima, 1960; Franklin & Lewontin, 1970) stresses that the situation may be very complex, even if only two loci are involved. Indeed, the evidence usually cannot exclude the operation of multilocus systems of very great complexity.

These remarks may bring to mind the polemics of Goldschmidt (1940), some 35 years ago. We need not, however, embrace the "chromosome as a whole" and reject the gene concept to invoke the existence of balanced blocks of interacting genes. I am fully aware that it is easy to play a somewhat pontifical role in this field, accusing the mathematically-inclined of oversimplification and advancing as a substitute theories of "shifting balance." I do it not in an effort to denigrate the work of others but rather in an attempt to stimulate study of these more complex and subtle phenomena by those who possess the practical tools and theoretical orientation to do so.

In the last few years, several situations have come to light which suggest a new approach to a more realistic unit of selection (or unit of random drift, for that matter). For example, Carson (1967, 1973) and Carson et al. (1969) have shown that, under selection, some strains of the normally bisexual species *Drosophila mercatorum* will give rise to vigorous and self-sustaining laboratory stocks which reproduce wholly without males. By rather simple genetic methods, it was shown that not only are the females which comprise such a stock diploid but

also that the stock acquires a completely isogenic state. How can the genotype of a normal bisexual species become so readjusted as to permit its carriers to survive and reproduce despite the vigors imposed by a complete and total homozygosity? Sing & Templeton (1975), and Templeton et al. (1976a, 1976b) have provided evidence that the capacity of these strains to reproduce in this manner is based on a multilocus genetic organization or coadaptation of genes which permits such total homozygosity. Development and reproduction are impaired if this coadaptation is perturbed by recombination away from a particular internally balanced state. Selection back to the original coadapted state occurs largely at the zygotic stage. Perturbation of even small sections of the genome give evidence of the existence of a true coadaptation involving nonadditive interactions between nonalleles. The capacity for parthenogenesis in these stocks, therefore, is related to a complex genetic organization of genes of individually minor or insignificant effects.

The importance of the Sing and Templeton work, which is just beginning, is that it provides a new technique for analyzing the unit of selection with great sensitivity. The model they have adduced would appear to have wide application to the understanding of gene interaction in all kinds of diploid systems. The parthenogenetic system that they have used merely provides an elegant tool for the stabilization and then dissection of the underlying genetic state.

In considering the genetic basis for adaptive change in populations, these balance theories have another important implication. The entire genome of the species is not under obligation to mount a response to selective pressure from the external environment. Goodhart (1963), Clarke & Murray (1971) and Jones (1973) have urged that greater attention be given to "area effects" wherein certain local areas show unique and persistent epistatic relationships between genes. Thus local climatic selection may find itself working on a genetic environment which is, because of epistatic balance, somewhat refractory to a quick and simple genetic response. In a recent paper (Carson, 1975) I have suggested that some of the assumed relationally balanced polygenic blocks in a species may become essentially fixed species-characteristics which are closed to recombination because of the inviability or biological inefficiency of the crossover products. The prevailing view that the thousands of loci along a chromosome are all available in any combination seems to me simplistic and not in accord with the data surrounding the various kinds of natural and artificial selection.

To what extent is the allozymic variation carried within a species relevant to the type of adaptational adjustments just discussed? This complex question may be approached by comparing local populations within a species to see how closely such variation tracks the ecological diversity within the species range. Indeed, direct correspondence appears to be very low. Many species show a remarkable genetic similarity between their local geographical populations despite wide differences in geography and ecology (Prakash et al., 1969; Prakash, 1973; Ayala et al., 1972). Both Mukai et al. (1974) and Zouros (1975) have questioned whether allozymic variation is maintained by balancing selection.

In these studies and similar ones, a very useful method of data-reduction has been employed, namely, the indices of genetic similarity (or distance) between

pairs of populations (e.g., Nei, 1972; Rogers, 1972). When compared, local populations of the same species tend to show a similarity index of 0.95 or above (1.0 would indicate identity). This very remarkable similarity between such populations suggests that the allozymic variability does not form the basis for a simple and direct relationship between microadaptation and allozymic loci. In artificial populations of *D. willistoni*, Powell (1973) observed frequency changes in alleles at allozyme loci, but he is careful to point out that these changes might be due to the association of these loci with larger gene blocks, such as inversions. Accordingly, the old problem as to what is the unit of selection again appears.

In a similar manner, it is difficult to associate inversion variability with specific microadaptational response. Inversions, unlike most allozyme polymorphisms, frequently show geographical clines and artificial selection sometimes elicits a response from these chromosome variants. On the other hand, as has been argued by Dobzhansky and others, it appears to be coadaptive gene balances which change geographically. After all, inversions are gene blocks. When they undergo significant frequency changes with altitude, temperature or other environmental parameters, hundreds of gene loci are undoubtedly involved in the geographical shift.

Inversions, furthermore, are dispensable in microevolution. Among 95 Hawaiian picture-winged *Drosophila* species assayed for inversion variability, 65 (68%) show no intraspecific inversions whatsoever (Clayton et al., 1972). Indeed, this shows that adaptive microevolution does not require segregating cytological variation, because only one-third of the species studied exploit the advantages of inversions, whatever these advantages are.

In cases of species where both allozymic and chromosomal variability is present, local populations appear to show more differentiation in chromosomes than in allozymes (Prakash, 1973; Carson et al., 1975). This may be because the inversion, on the average, can embrace and thus mark a larger "chunk" of the genome than the allozyme locus.

In conclusion, selection appears to effect a genetic response by favoring various balanced combinations of genes. Single loci are rarely favored *per se* but mainly as part of an interacting group of genes. Not all of the genetic material of the species is open to the recombinational system which generates the balances that selection operates on. Inversions are dispensable to the functioning of the process but, when present, they form an efficient means for developing and holding epistatically balanced gene blocks.

SPECIATION

This process contrasts with anagenesis in that a branching, or cladistic, event is involved. What was formerly a single population splits into two and these subsequently come to be recognized as different biological species. Unlike anagenesis, cladogenesis has been rather refractory to analysis.

Part of the difficulty lies in interpreting the time of origin of the genetic differences displayed by the two species. Some, if not most, of the differences that we observe have undoubtedly been added after the cladistic event has taken place and, accordingly, are not relevant. If we could recognize this category of

differences and subtract them, we would be left with the crucial syndrome of differences which arose synchronously with the cladogenetic events. This might lead to a simplification of the problem; an attempt in this direction will be adduced later in this section.

For reasons set forth in several recent publications (Carson, 1970, 1971, 1975) I have questioned whether speciation is universally the outcome of a direct response to an environmental need. Have the genetic changes which accompany speciation been established under selective control and in the same manner as discussed above for adaptation? These considerations are based on observations drawn from various exuberantly speciated insular biotas. These facts suggest that species-splitting is consequent on a sudden strong geographical isolating event such as occurs when a daughter population is founded, allopatrically to the progenitor population, from one or very few individuals.

Under these circumstances, speciation may have a strong stochastic element. The new isolated population is forced, perhaps because of the attenuation and disruption of the old gene pool at the founder event, to evolve a new system of internal genetic balances. Incipient reproductive isolation could be initiated as a chance accompaniment of this process. This forced reorganization of the genome may be initially established by selection for a new kind of genetic balance rather than representing any tracking of external environment. The latter, as well as the completion of isolation, would be expected to follow, rather than be synchronous with, the cladistic event.

In discussing reorganization in anagenesis, mention was made of the many such changes observed by Templeton et al. (1976a, 1976b) as parthenogenetic strains are formed. Similar genetic revolutions (see Mayr, 1954, and Carson, 1975) may indeed be important as an early stage of speciation. Lewis & Raven (1958) and Gottlieb (1974) have stressed the element of chance in certain plant speciation patterns.

A more traditional view of geographic speciation calls for the gradual formation of species through a geographical subspecies as an intermediate stage. This occurs because allopatric populations of the same species may become genetically differentiated as a consequence of their adaptation to different environments. A second stage of the process calls for selection which favors reproductive isolation between the two genetically differentiated populations. Subspecies which have acquired incomplete biological isolating mechanisms are sometimes referred to as semispecies. Only when reproductive isolation is complete can full specific status be assumed.

As a paradigm of this gradual speciation process, Ayala et al. (1974) have adduced the case of the *willistoni* group of *Drosophila*. They recognize five increasingly divergent levels of cladogenesis. These may be observed by comparisons (1) between geographic populations within a species, (2) between subspecies, (3) between semispecies, (4) between sibling species, and (5) between morphologically distinguishable species of the same group. These authors have suggested that the allozymic genetic differences accumulate gradually over these levels of divergence. Thus, whereas local populations show allozyme similarity indices of about 0.97, subspecies and semispecies average 0.8 similarity when

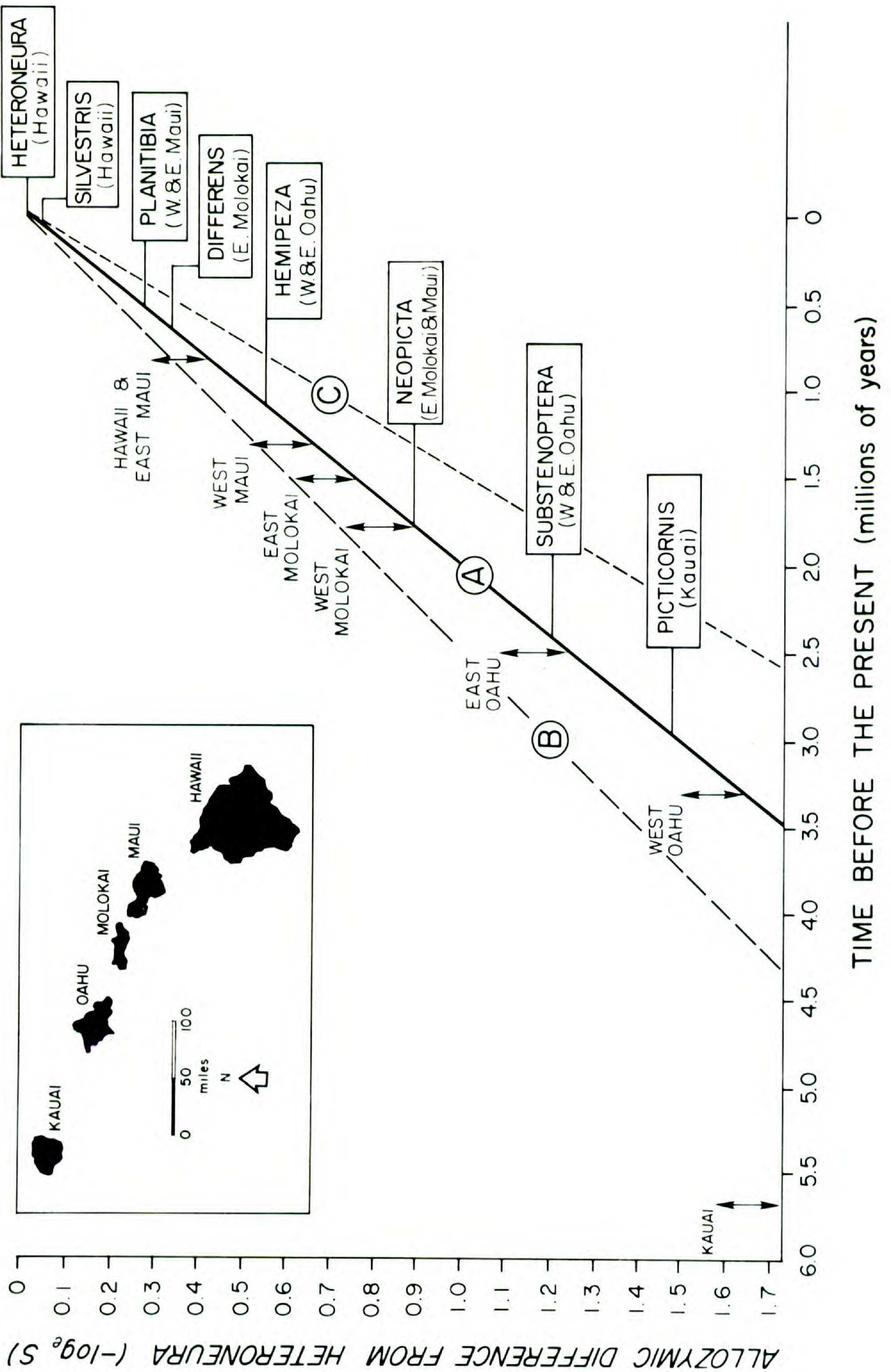
examined by pairs. Sibling species show a similarity of about 0.5 and nonsibling species about 0.35. These indices are based on allozymes alone; other kinds of genetic differences are not taken into account. In the *willistoni* group, semispecies seem not to differ in their allozymic similarities from subspecies. Ayala et al. interpret this to mean that the initial isolations depend on a rather small number of genes.

Although the above scheme seems to fit the *willistoni* group rather well, it appears not to fit certain other *Drosophila* situations, notably the Hawaiian *Drosophila*. Johnson et al. (1975), for example, have calculated similarity coefficients based on allozymes for sixteen species of the *planitibia* subgroup. Two of them (*D. heteroneura* and *D. silvestris*) are endemic to the geologically very recent Island of Hawaii. These two new species are strikingly different in color and morphology and coexist sympatrically. They show an allozymic similarity coefficient of 0.96, similar to the level shown for intraspecific local populations of the members of the *willistoni* group. Such very high allozyme similarities are also found between some other pairs of species of the *planitibia* subgroup on the Island of Maui (Johnson et al., 1975). A similar situation obtains for another pair of sympatric species, of a different subgroup, for Hawaii Island (Carson et al., 1975). In both of these cases, morphology and chromosomal characters are more efficient in differentiating species than are the electrophoretic differences.

Soluble protein (allozymic) differences have been shown to be minimal between species in a number of other cases. Thus, Turner (1974) found minimal divergence among five species of pupfish from the Western United States; Koehn (1967) obtained similar results. Avise (1975) reports that several species-pairs of *Peromyscus* show similarity coefficients above 0.95 and Avise et al. (1975) find that the same is true of two California minnows (*Hesperoleucus symmetricus* and *Lavinia exilicauda*). These have been referred by systematists to different genera! King & Wilson (1975) have assembled a large amount of data which show that man and chimpanzee, likewise assigned to different genera, are as similar to one another biochemically as a pair of sibling species of *Drosophila*. Certain plants show a similar pattern. Thus Gottleib (1973, 1974) has found very close allozymic similarities between species-pairs in *Clarkia* and in *Stephanomeria*.

Accordingly, it appears that in a number of cases speciation can occur without significant alteration in genetically-determined soluble proteins. It is also well documented in the data on Hawaiian *Drosophila* that many closely related species are homosequential in all of the polytene chromosomes (see Clayton et al., 1972), indicating that speciation can indeed occur without sequential alteration or indeed any participation by inversions or translocations in the process. Even genes which determine external morphology may remain basically unchanged as in the well-studied cases of sibling or morphologically cryptic species in many sections of the genus *Drosophila*.

Thus, to sum up the present argument, crucial cases exist showing that speciation in diploids can proceed without significant alteration in structural chromosome sequence, soluble proteins, or the genetic basis of external morphology. Differential adaptation is not a prerequisite. This brings us again to the concept



of polygenic balance, which was discussed earlier, and to the subject of gene regulation. The latter concept has been recently invoked to explain important evolutionary changes. Wilson et al. (1974), for example, “. . . regard adaptive evolution as resulting primarily from changes in the expression of genes relative to one another rather than from amino-acid substitutions in the products of those genes.”

Direct knowledge of gene regulation in eukaryotic systems is exceedingly rudimentary. Extrapolation from the elegant systems which are known in prokaryotes are widely made but should be viewed with caution. This will not be the first time, however, that evolutionary genetics has been forced to consider developmental control of the phenotypes on which the evolutionary process operates.

ELECTROPHORETIC DATA AS AN EVOLUTIONARY CLOCK

Much attention has been given in recent years to the interpretation of protein evolution through amino-acid substitution (e.g., Fitch, 1972; Langley & Fitch, 1974). At the level of the species population, furthermore, strong arguments have been advanced that the allozymic variation is neutral or quasi-neutral to selection (for a recent formulation, see Ohta & Kimura, 1975; see also Zouros, 1975). Accordingly, there may also be a direct correlation between high allozymic similarity and the recency of the cladistic event which separated the two compared entities.

A line of evidence suggesting such a passive role for allozymic differences in evolution is provided by some data cited by Avise & Ayala (1975, 1976). The North American minnows (family Cyprinidae) are highly species-rich. Since the late Miocene, some 250 species have been formed. Although evolving over similar geologic time, the sunfish genus *Lepomis* is species-poor, having produced a total of only 11 species. Differential extinction rates in the two phylads can apparently be ruled out. Avise and Ayala ask whether the mean allozymic difference between existing species is related to the number of cladistic events in the phylad or whether it is a function of time since the first cladistic event. The coefficients are remarkably similar when the products of the species-rich and species-poor phylads are compared. The authors conclude that time since divergence from a common ancestor is more important than the number of intermediate cladistic events in determining the level of allozymic divergence between species.

If decay of similarity is progressive and related to the length of time since the

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FIGURE 1. Allozymic difference and time of species origin in eight species of Hawaiian *Drosophila* (*planitibia* subgroup). Allozyme differences (pairwise comparisons with *D. heteroneura*) are plotted against the age of the oldest recorded rocks of each island or volcano. Under each species name is indicated the island (or volcano) to which that species is endemic. Diagonal line A assumes a uniform accumulation of difference of 1% each 20,000 years. From this, the time of each past species origin is predicted. Diagonal B represents a slower rate of change (1% difference in 25,000 years). Diagonal C assumes faster change (1% difference in 15,000 years). Diagonal A gives the most satisfactory fit to the geological and geographical data.

ancestral splitting, allozymic differences might be used in some circumstances as a clock to determine evolutionary rates and, indeed, the time of past cladistic events. An example may be taken from certain *Drosophila* species of the Hawaiian Islands (Carson, 1976). The ages of five of the largest and most southeasterly Hawaiian islands are accurately known from magnetic declination and potassium-argon data (Macdonald & Abbott, 1970). One of the two sympatric species of the *Drosophila planitibia* subgroup endemic to the geologically most recent Island of Hawaii (*D. heteroneura*) may be compared by pairs with seven of its close relatives for allozyme similarity (S values of Rogers; see Johnson et al., 1975). Assuming that allozymic genetic difference accumulates at a uniform rate, the coefficients of genetic difference ($D = -\log_e S$) of these seven from *heteroneura* may be plotted against time as indicated by the age of the islands to which these flies are endemic (Fig. 1).

An assumed rate of accumulation of genetic difference of 1% in 20,000 years fits the ages of the islands and the inferred times of cladogenesis rather well. Faster or slower differentiation (i.e., 1% in 15,000 or 1% in 25,000 years) produces a less satisfactory fit of the data to the geological and biological facts (Fig. 1). These observations are in line with the idea, stated earlier in this paper, that speciation has an initial stochastic element. Thus, the Hawaiian *Drosophila* of the Island of Hawaii, the pupfish of Death Valley, the cyprinid minnows of California, and *Clarkia biloba* and *C. lingulata* may all be examples of recent speciation. They may have not had enough time to accumulate much allozymic difference. According to this view, the members of the continentally distributed *willistoni* group of *Drosophila* species diverged from one another in the much more distant past so that allozymic differentiation between some subspecies, for example, is greater than that between species in the other very newly formed taxa mentioned above.

CONCLUSION

Numerous cases exist wherein both speciation and adaptation can proceed in the absence of genetic fixation involving allozymes, chromosomal aberrations, heterochromatin differences, "visible" genes, lethals and morphological differences. If no one of these various known types of genetic variation is an absolute requirement, it follows that we must look elsewhere for an underlying common genetic element. The suggestion is made in this paper that evolution has, as its common denominator, a shifting internal balance of gene interactions in which a strong role is played by regulatory genes. Such a formulation can be invoked to explain the stochastic nature of some speciations following founder events. Although allozymic variation may be trivial with regard to selection, it may turn out to be useful as a clock from which we may read the age of a species.

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